12.

A Study of the Social Behavior of a Captive Herd of Giant Tortoises.

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(Text-figures 1-4).

Introduction.

This study of the social behavior of the giant tortoise, *Testudo elephantopus*, was made to discover whether any hierarchical social structure existed in the herd of 14 Galapagos tortoises at the New York Zoological Park. These particular animals were favorable subjects for a psychological study because they had lived together a long time and their environment at the Park was relatively static.

Van Denburgh's report (1914) sheds important light upon the habits of these great tortoises in their natural haunts. The following excerpts are taken directly from his monograph. ". . . When I landed at Chatham Island, . . . near the springs, it was a curious spectacle to behold many of these huge creatures, one set eagerly travelling onward with outstretched necks, and another returning, after having drunk their full. . . . The inhabitants say each animal stays 3 or 4 days near water, and then returns to the lower country; from observing marked individuals, they say the tortoises travel a distance of about 8 miles in 2 or 3 days. One large specimen which I watched, walked at the rate of 60 yards in 10 minutes, that is 360 yards an hour, or 4 miles a day, allowing a little time for it to eat on the road.

"Most travelling is done early in the morning and late in the afternoon, the hot hours of noon being spent in the shade of a bush, wallowing in the damp soil. . . . All of the species we observed make seasonal vertical migrations. Soon after the rainy season starts they descend the mountains to the grass-covered flats at their bases to feed and deposit their eggs in the light soil. After the grass is withered, they again ascend the mountains to the moist meadows produced by the trade winds at an elevation of 2,000 feet and above.

"These migrations are most marked in the dry regions, as at Tagus Cove, Albemarle Island; but even at Iguana Cove (same Island), where there is an abundance of moisture at lower elevations, a nearly complete migration takes place. . . . In their seasonal pilgrimages they follow well established trails used perhaps for generations. These trails radiate from the higher plateaus as a center and usually follow the floors of the canyons to the flats below. Some of the trails are of considerable length, requiring several days of persistent effort on the part of the tortoise to cover them." Beck (1903) confirms Van Denburgh's description of the habits and environment of these huge creatures.

Most herpetologists agree that all Galapagos tortoises belong to one species, *Testudo elephantopus*. Those found on the different islands of the archipelago represent subspecies. Because of the close resemblance between *T. elephantopus* and the large South American tortoise, *Testudo denticulata*, it is believed that the mainland form was transported to the islands on floating trees in the wake of the prevailing westerlies, countless centuries ago.

Townsend (1925) has shown that tremendous numbers of turtles existed at one time on the Galapagos Islands. Several lines of evidence indicate that the animals moved in herds. The deeply worn trails, only wide enough for one animal to pass, radiate in all directions downward from the higher elevations. The tortoises travelled these trails in tandem fashion, one behind the other. This enforced a type of social hierarchical rating, since only one individual could lead a herd and each member of the group had to keep its place in line or actually prevent those behind from passing, in many parts of the trail. In other words, the social behavior of the species was modified in response to the very rocky terrain. The present study attempted to determine whether the same social patterning, or a modification, is reflected by individuals in captivity.

Procedure and Description.

Prior to 1946 the New York Zoological Park herd consisted of eight specimens. Two of these, a male (designated as YO) and a female (designated as YD), were from the Aldabra Islands. The remaining six tortoises were originally from the Galapagos Islands.

[1] In these experiments the authors had the assistance of D. Burckhardt and J. A. Murnin who, with the authors, held Animal Behavior Fellowships of the New York Zoological Society for the summer of 1949. See abstracts of papers read by the Fellows before the Animal Behavior and Sociobiology Section of the American Society of Zoologists, December 28, 29, 30, 1949, in *Anat. Rec.*, vol. 105, no. 3, pp. 25-31, 98-102. Wholehearted cooperation was received from the late Brayton Eddy, Curator of Reptiles at the New York Zoological Park; Keeper Earl Chace and Staff Photographer Sam Dunton. The senior author wishes to thank also Mr. Charles M. Bogert for helpful advice.

TABLE 1.

Physical Measurements of Giant Tortoises (October 14, 1949).

Species	Name	Sex*	SL†	CL	SW	CW	Height	Wt. lbs.	No.
T. e. vicina	RO	m	39	52	29	48½	20	343½	146
"	RX	m	40	53	29½	53	23	331½	186
"	RT‡	m	42	53	29	54	22	328½	128
"	R=	m	34	46	26	48½	18	268	162
"	Y=	f	31	43	24	44	17	210¼	180
"	RD	f	28	40	22	43	16½	196	83
"	YX§	f	23	28	18	34	13	92½	A3
T. e. vandenburghi	BT	m	37	50	23	49	18	275½	A6
"	BO	m	33	45	24	43½	18	241½	A7
"	YT	f	27	37½	20	37	16	150	A8
T. e. ephippium	RH	m	26	30	19	31	12	111	A5
"	BX	m	23	28	18	27½	11½	81½	A4
T. e. aldabra	YO	m	32	36	24	38	11	182	A1
"	YD	f	30	41	21	42	14	168	A2

* The male has a concave plastron and its tail is longer than that of the female.
† SL—Straight length of carapace in inches.
CL—Curved length of carapace in inches. (Measured over the curve of the carapace).
SW—Straight width of carapace in inches.
CW—Curved width of carapace in inches. (Measured over the curve of the carapace).
Height—in inches.
‡ RT—Weight at death, December 3, 1949, was 307 pounds.
§ YX—*T. e. nigra*.

Two of these were so-called saddle-back males, *T. e. ephippium* (RH and BX). Three, two males and a female (BT, BO, and YT), belonged to the *vandenburghi* subspecies. The sixth specimen, a female (YX), was *T. e. nigra*.

In 1946 the Curator of Reptiles, the late Mr. Brayton Eddy, brought 6 specimens of *T. e. vicina* from Florida. These comprised four large males (RT, RX, RO, and R=) and two females (RD, and Y=), part of a herd of 180 giant tortoises brought from the Galapagos in 1928 by C. H. Townsend, then Director of the New York Aquarium.

Since the arrival of the *vicina* specimens at the Park, they have been housed with the other eight tortoises at the Reptile House. The entire herd of 14 was fed and watered together and enjoyed the same exercising yard and sleeping quarters.[2] On December 3, 1949, a large male, RT, died. Autopsy revealed a mass of unchewed carrots in the intestine, which might have caused an obstruction to the passage of food. Table 1 gives the physical measurements and permanent number of each specimen studied.

The degree of sociability[3] of the herd was noted by recording, by means of diagrams, the positions which individual tortoises took with reference to other individuals in the following four habitual resting situations: at evening rest in the shelter, or P pattern (for P.M.); at morning rest in the shelter or A pattern (for A.M.); when clustered around the piles of lettuce outside the shelter, or L pattern; and while sunning, or S pattern.

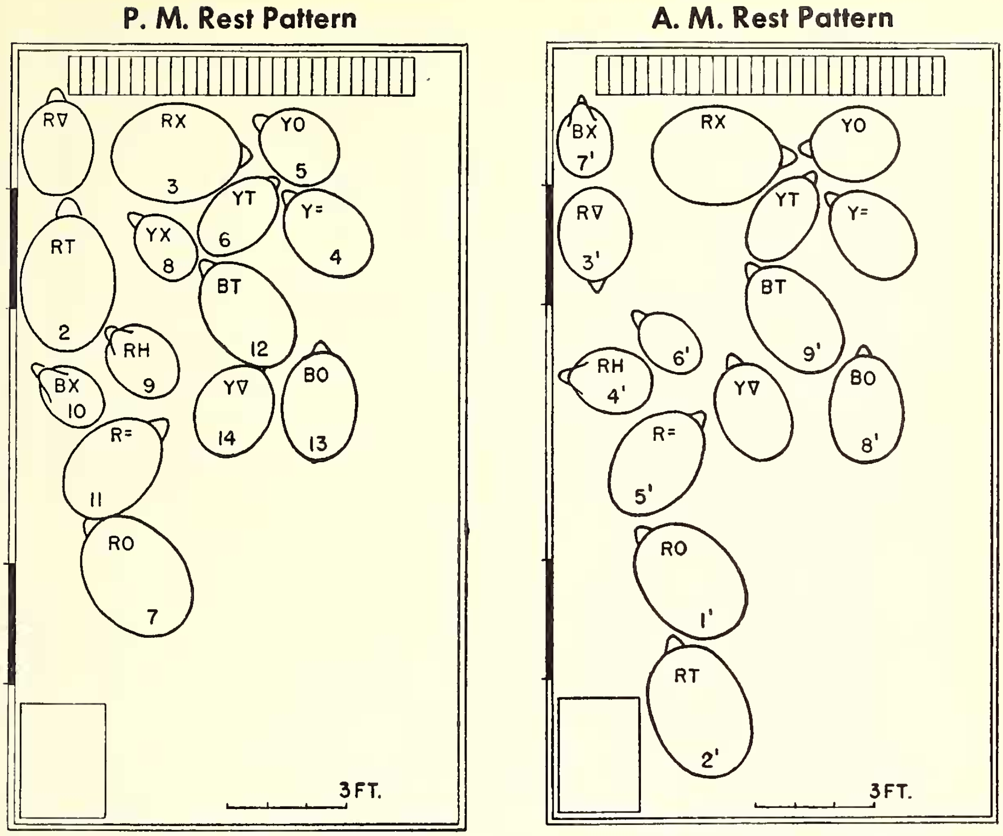
Daily records of these four categories of social contacts were kept for an average of 28 days. In addition, an average of 40 daily records were preserved of the order in which each animal entered the shelter for the night and emerged from the sleeping quarters in the morning. Instances in which individuals failed to enter the shelter in the evening voluntarily, or remained inside in the morning, were likewise tabulated.

For the safety of the herd it was necessary to lock it in the shelter each night and those animals which failed to go in of their own accord by 4:30 P.M. were gently urged inside by the keeper. Half an hour was allowed for the herd to settle down, after the door was closed, before the evening rest pattern was recorded. Occasional inspections as late as 10 P.M. showed virtually no change from the 5 P.M. pattern. The commonest change recorded in this interval was a partial rotation of the animal on its own axis so that it faced another direction, but remained in essentially the same relation to its shelter mates.

Text-figure 1 depicts the actual evening rest pattern on July 7, 1949, and the morning rest pattern of July 8, 1949. It is a typical example and displays many social contacts characteristic of individual animals. The

[2] The summer sleeping quarters in the shelter measured 19 feet 6 inches by 14 feet 2 inches. The winter housing was the same for the eight large specimens, while the adjoining inside corral accommodated the six small specimens (YD, YT, RH, YX, BX, YO). The outside yard was 43 feet 4 inches by 26 feet 2 inches, with the south end rounded. Winter temperatures (below about 63°F.) make it necessary to provide heated quarters indoors for these giant reptiles between the months of October and April.

[3] The term "sociable" or "social" as used in this report denotes an endogenous urge on the part of one tortoise to be close to another. It does not refer to sexual or fighting contacts. To eliminate as many random meetings or contacts as possible between individuals, only those contacts were recorded that occurred when two animals were together, their shells touching or a few inches apart, in an attitude of rest with plastrons on the ground.



TEXT-FIG. 1. The actual evening and morning rest patterns of July 7 and July 8, 1949, respectively. The carapaces of the herd are shown in correct scale with reference to the size of the shelter and to each other. The numerals on each tortoise in the P. M. Rest Pattern indicate the order in which each entered the shelter in the evening; those on nine specimens in the A. M. Rest Pattern indicate the order of exit in the morning. The remaining five tortoises left the shelter about an hour later.

The contacts recorded on these two specific occasions are given to illustrate the technique adopted in recording all the contacts as given in Table 2.

P pattern: RD-RT, RD-RX, R=-RO, BT-BO, BT-YT, YD-BO, R=-YX, YO-Y=, Y=-YT, R=-RH, RT-RH; these 11 were significant (see Table 2). The following proved to be random (see Table 2): R=-BX, BX-RH, YX-YT, YX-RX, YT-YO, RX-YT, BT-YD, RX-YO.

A pattern: RT-RO, R=-RO, R=-RH, BT-YT, BT-BO, R=-YX; these were significant (Table 2). The following were random contacts (Table 2): R=-RH, YX-RH, BX-RD, RX-YT, RX-YO, Y=-YO, Y=-YT, YD-BT, YD-YX. The grill at the upper end of each diagram represents the radiator.

outlines of the carapaces of the several members of the herd are shown in correct scale with reference to the size of the shelter and to each other. In the diagram of the P.M. Rest Pattern, the number on each carapace denotes the numerical order in which each tortoise entered the shelter via the door at the lower left, near the rectangular water pan. In the diagram of the A.M. Rest Pattern, the numbers, primed, on nine individuals, indicate the order in which they emerged from the shelter when the door was opened on the following morning. Five members of the herd failed to leave the shelter until very much later in the day, when they were gently urged out by the keeper before he proceeded to clean the shelter. Almost all defecation occurred indoors, usually early in the morning.

Text-figure 1 summarizes graphically the habitual behavioral traits of several members of the herd. By comparing the P and A patterns it will be observed that RD was the first to enter the shelter on this particular evening, that she chose the left hand corner by the radiator, and that she left the shelter in third place. To do so she had to thread her way around and perhaps over certain other animals.

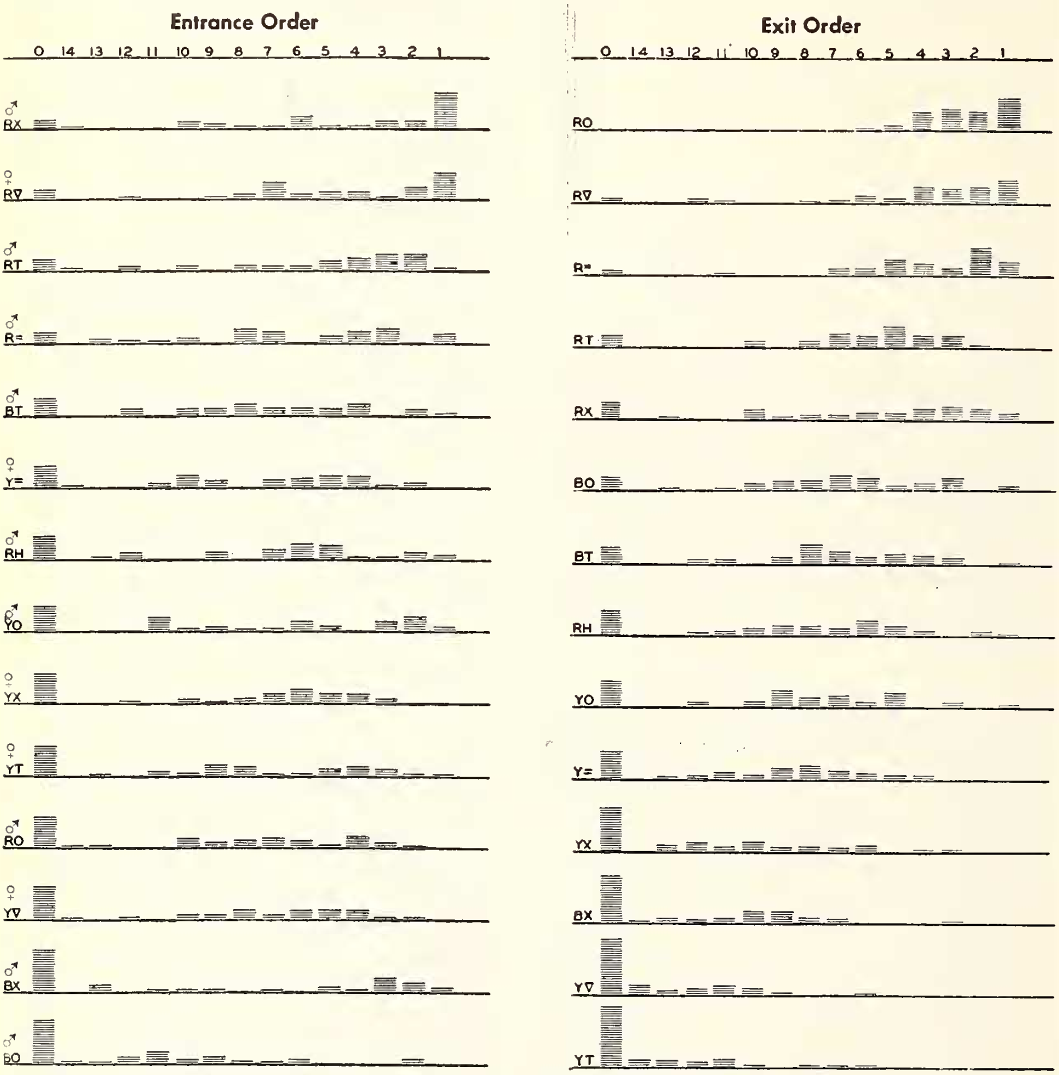
RT entered in second place, coming to rest immediately behind RD. In the morning he moved to the water pan, indicating that he climbed over or shoved his way between individuals to reach his goal. RT left the shelter also in second place, directly behind RO.

RX entered the shelter in third place, resting next to RD, against the radiator. RX usually sought the left hand corner but on this particular evening RD reached it first. RX made almost no change in position during the early morning hours and did not leave the shelter until urged by the keeper.

RO's morning position was relatively unchanged from that of the evening position. RO habitually entered the shelter after many or most of the others had done so or after being prompted by the keeper. RO invariably came to rest by the exit door. On July 8 he departed in the morning in first place.

Although RO and BO preferred to enter the shelter after most of the others had done so, the numerical order of exit of each was quite different. RO left habitually in first place; BO habitually rested by BT and departed usually in sixth place, after most of the largest tortoises had done so. The relative positions of the other members of the herd in Text-figure 1 will not be analyzed at this point but the relative sociability of all the herd will be examined later.

Text-figure 2 depicts the actual performance of each member of the herd with reference to the numerical order of entrance and exit for a total of 40 and 42 days, respectively. The vertical column marked "0" represents the number of failures of any individual to enter or leave the shelter of its own accord. Text-figure 2 especially emphasizes the following: 1. Individuals that are prone to enter or leave early in numerical order show relatively few failures to enter or leave; there are cases, however, in which a tortoise entered early in numerical order but departed late; such an individual usually had more failures in departure than in entrance. The reverse would apply to a tortoise which entered late but emerged early. 2. Tortoises that habitually enter or leave late in numeri-



TEXT-FIG. 2. Depicts the number of times each member of the herd entered or left the shelter during 40 evenings and 42 mornings, respectively, in each of 14 possible numerical positions of precedence. The columns marked "0" record the number of times each individual failed of its own accord to enter by 4:30 P.M. or to leave by 10 A.M.

cal order show many failures to enter or emerge. 3. There was greater consistency on the part of individuals in the exit order than in the order of entrance. This was in part due to the greater number of distractions outside the shelter in the afternoon than inside in the morning. There was also a growing urgency to be active after a night's sleep and perhaps to escape the nightly accumulation of excreta.

Specific examples may be cited in connection with Text-figure 2. It has been mentioned that RO was prompt to leave the shelter; this is correlated with the fact that he stayed near the door while inside. He was naturally in a favorable position to emerge first, which he did on 14 mornings. During the remaining 18 mornings his numerical order of exit was never greater than sixth and was usually second, third or fourth. RO never had to be urged out by the keeper. In contrast, RO usually entered the barn in eleventh place and on 13 evenings he failed to enter by 4:30 o'clock.

RX seemed to be particularly anxious to enter the barn early in the afternoon. Text-figure 2 indicates that although he ranked fifth in order of exit, he ranked first in order of entrance, having preceded the herd on 15 evenings and failing to enter a minimum of four times. RX was a dominating male and generally managed to secure his share of food by merely shoving in and taking it. Others in the group usually withdrew when RX reached for a morsel.

RD was surprisingly consistent in both her entrance and exit patterns, ranking second in both. She was either very sociable or restless, settling down with one group or individual, then with another, then with a third; subsequently she would enter the pool, drink deeply, crawl out and walk along the fence. She seemed to have a rather aggressive attitude toward others; she rarely yielded or retired in favor of any but the three largest males.

RT followed a surprising pattern. He regularly followed RD or RX in and followed RD, RO or R$^{=}$ out of the shelter. Thus RT was rarely first in or out, but was apt to enter or leave the shelter early in the numerical order. RT not only followed RD or RX in, but chose to rest immediately next to one or the other throughout the night.

R$^{=}$ behaved like RT but with slightly less consistency. This male habitually followed RX and RD into the shelter and emerged in the morning usually immediately after RO or RD. Like RT, R$^{=}$ found satisfaction in being with the individuals mentioned. When they moved from sight, he exhibited a strong urge to go to them.

The actions of the two big males of the *vandenburghi* race deserve attention. It will be noted that their numerical order of exit is similar. Each male was closely observant of the other and also of the larger *vicina* tortoises. The *vandenburghi* males rarely left the shelter before the latter did so and then BO usually preceded BT in his exit.

The entrance pattern of BT and BO was quite different. BT entered the barn after most of the larger tortoises had done so, usually in fifth place. BO, on the other hand, either failed to enter without urging by the keeper or else very late in numerical order. He seemed to be particularly responsive to the crowds of visitors passing the outside pen just before the Zoological Park's closing time. He stayed near the fence and kept busy eating the sweetened popcorn tossed to him.

The numerical order of entrance and exit of the two saddle-back males was quite different. While RH was usually seventh in and eighth out, BX was thirteenth in and twelfth out. The numerical positions of these tortoises are, no doubt, a reflection of the antagonistic behavior of RH toward BX. The former would raise his head, open his beak-like jaws, and stalk slowly toward BX whenever the latter approached. BX invariably retreated.

The first place position of RO in the Exit Order (Text-fig. 2) and his position in eleventh place in the Entrance Order relates closely to the degree of sociability recorded between RO and RT, RX, R$^{=}$ and RD, in the P and A patterns (Table 2). It will be observed that of a total of 149 social contacts between these five individuals in the A pattern, 65, or 43%, were between RO and the other four, while in the P pattern only 83 were recorded and of these only 14, or 16.6%, were between RO and one other, the association being RO-R$^{=}$.

It is apparent that the tardiness of RO to enter the shelter at night, as well as his habit of sleeping close to the door, separated him from the other four in the P pattern. In the morning the others shoved between and climbed over intervening animals to come to rest close by RO, in the A pattern. When the door was opened RO usually crawled out first, followed closely in order by RD, R$^{=}$ and perhaps even RX, and only then by RT.

When RX entered the shelter first, which he usually did, he was able to occupy his favorite corner. RD followed immediately, or less usually preceded RX. RT consistently followed RD or RX, preceding them only once in 40 evenings. R$^{=}$ rather habitually followed RT, and RO entered about eleventh in line. As each tortoise entered it moved resolutely to its accustomed sleeping spot, RD immediately beside RX (19 times), RT beside RX (22 times), R$^{=}$ immediately behind RT (14 times) but not near RD or RX, and finally RO immediately behind R$^{=}$ (14 times), with male RO resting close to the door.

Table 2 records every contact made between each of the 14 tortoises with every other member of the herd for a total of 28 days, for each of the four resting patterns (P, A, L, S). In analyzing these data it is necessary to distinguish random contacts between individuals from contacts resulting

TABLE 2.

Total Number of Contacts During 28 Days Between All Tortoises in Each of Four Rest Patterns.

	Pattern	RT	RX	RO	R=	RD	Y=	YX	BT	BO	YT	RH	BX	YO	YD
RX	P	22													
	A	16													
	L	7													
	S	13													
RO	P	6	4												
	A	22	17												
	L	8	8												
	S	20	14												
R=	P	14	7	14											
	A	17	15	15											
	L	11	6	8											
	S	17	17	13											
RD	P	14	19	5	4										
	A	14	11	11	11										
	L	8	8	5	6										
	S	9	16	15	9										
Y=	P	18	10	11	14	7									
	A	12	13	9	16	9									
	L	5	3	6	9	8									
	S	7	11	7	11	7									
YX	P	8	10	6	14	3	9								
	A	5	6	0	13	3	10								
	L	7	5	9	1	6	4								
	S	4	6	2	2	3	2								
BT	P	14	10	7	12	14	10	10							
	A	6	8	6	12	9	8	11							
	L	14	11	10	4	6	8	9							
	S	4	2	3	4	2	7	7							
BO	P	16	2	13	12	6	17	12	15						
	A	13	4	10	13	9	10	10	14						
	L	7	4	8	8	10	10	8	12						
	S	9	7	12	6	13	9	3	15						
YT	P	8	9	7	7	8	12	8	11	7					
	A	7	5	7	7	13	9	13	11	13					
	L	6	5	3	2	6	4	3	9	8					
	S	2	1	1	2	1	6	1	9	4					
RH	P	11	8	4	12	9	11	8	9	7	9				
	A	5	10	5	6	20	11	9	9	13	10				
	L	2	10	4	2	8	7	9	2	4	5				
	S	4	1	6	2	5	1	1	5	2	4				
BX	P	6	7	7	7	8	3	6	3	5	7	9			
	A	6	6	4	5	3	6	15	10	5	15	7			
	L	2	8	1	3	1	3	7	3	5	4	3			
	S	4	9	1	3	3	4	7	2	6	1	4			
YO	P	11	9	6	6	4	15	9	6	9	5	4	10		
	A	6	5	7	10	10	6	10	10	8	8	6	11		
	L	7	2	4	6	4	5	5	2	8	3	4	5		
	S	2	3	2	2	4	4	2	2	2	4	1	4		
YD	P	11	9	14	7	7	8	7	5	11	7	6	2	3	
	A	15	9	11	6	7	11	8	10	14	8	5	2	7	
	L	11	4	2	2	4	7	7	5	3	7	7	6	5	
	S	2	7	7	3	1	1	1	1	4	1	4	3	1	

* P = Evening rest in shelter; A = morning rest in shelter; L = Lettuce-eating in outside yard at noon; S = Sunning pattern outside in forenoon.

Note, for example, that RT contacted RX 22, 16, 7, and 13 times respectively,i n the 4 rest patterns mentioned above. (P, A, L, S).

TABLE 3.

Tabulation of Contacts and Units, both Random and "Social," of the 14 Giant Tortoises.

	RT	R=	BO	RO	RX	Y=	RD	BT	YD	YT	RH	YX	BX	YO
1*	169	162	227	205	243	248	235	242	218	245	252	266	236	257
2†	326	273	228	202	195	183	171	166	98	88	78	78	41	37
3‡	0.51	0.59	0.99	1.01	1.24	1.35	1.37	1.45	2.22	2.78	3.23	3.40	5.75	6.94
4§	29	32	35	37	39	38	40	39	44	44	46	45	49	49
5‖	22	20	17	14	13	14	12	13	8	7	6	6	3	3
6¶	16	12	12	9	10	6	8	6	3	3	2	4	2	1
7**	8	4	2	2	6	3	2	0	0	0	0	0	0	0

* Total number of random contacts (less than 11 in any single resting pattern).
† Total number of "social" contacts (more than 10 in any single resting pattern).
‡ Quotient (random contacts divided by "social" contacts).
§ Number of random units (a random unit comprises 10 or less contacts).
‖ Number of "social" units (a "social" unit comprises 11 or more contacts).
¶ Number of "social" units of 13 or more contacts each.
** Number of "social" units of 16 or more contacts each.

from a "social" attraction that one individual had for another or a mutual attraction between two tortoises.

It seems evident that 22 contacts out of a possible 28 (see Table 2, RT-RO, A; or RT-RX, P) is above the random level. In fact, there is reason to believe that the minimum number of contacts above the random level is 11 (see Table 3). Hence, the term "social unit" is applied to 11 or more contacts recorded for any two individuals in any of the four rest patterns, as for example, R=-RT: P 14, A 17, L 11, S 17 (Table 2). The total "social score" of any individual is obtained by multiplying the number of social units by the number of contacts in each unit (row 2, Table 3).

The random score for each tortoise is secured by multiplying the number of random units (comprising less than 11 contacts between two specific tortoises) by the number of contacts in each random unit (row 1, Table 3). If the total number of random contacts per individual is divided by the total social score, a quotient is derived for each animal in the group which is a measure of its sociability when compared with that of others in the group (row 3, Table 3).

In row 4, Table 3, is given the number of random units tallied by each individual, while row 5 shows the social units recorded for each. Rows 6 and 7 give the number of social units of 13 or more contacts and 16 or more contacts each, respectively, as recorded for each member of the herd.

It will be noted in Table 3 that a break appears between BT and YD in the figures of rows 2, 3, 4, 5, 6 and 7; that is, between the eight larger turtles and the six smaller ones. Before examining individual performances, a comparison should be made between these two groups.

For example, the number of random contacts (row 1) of the larger specimens averaged 12.6% fewer than those of the smaller ones. The average number of random units was 36 for the larger and 46 for the smaller tortoises (Table 3), while the average number of contacts per random unit for the larger ones was 5.98, compared with 5.32 for the smaller group.

The number of "social" contacts (row 2) of the larger animals averaged 67.9% more than those of the smaller, while the average number of contacts per social unit for the larger ones was 13.78 compared with 12.80 for the smaller. The total of random contacts of the 8 big ones when divided by their total of social contacts yields a quotient of 1.06, compared with 4.05 for the 6 smaller turtles (row 3). The average number of social units among the larger animals was 15.7 compared with 5.5 for the smaller ones (row 5).

A comparison of the number of social units comprising 13 or more contacts each, shows that the former group averaged 9.87, the smaller group 2.5 (row 6). The larger group tallied an average of 3.37 social units of 16 or more contacts each, compared with none for the smaller group.

Additional evidence bearing upon the assumption that 11 contacts in each of the four rest patterns is above random assortment between two individuals, is noted by comparing the performances of RT and R=, and YD and YT, which were the most "sociable" in their respective groups, with the remaining six and four animals of these two groups, respectively. This is especially notable in comparing the number of 11-, 10-, and 9-contact units of these animals. For example, the four most "sociable" tortoises mentioned above averaged 3.75 of the 11-contact units each while the others averaged 3.3 units and 1.75 units, respectively. The average number of 10-contact units tallied by the four most "sociable" specimens was 3/4 unit and the combined average of the remaining 10 was four units. The average number of 9-contact units of the former was 2.75 while that of the latter was 4.7 units.

Table 4 analyzes the intra- and interspecies (or subspecies) contacts between giant tortoises. None of the contacts referred to as random or social were of the mounting type characteristic of mating. Only the behavior of the eight largest specimens is given in Table 4, since their activities were most

TABLE 4.

Number of Social Contacts and Social Units* of Each of the Eight Largest Tortoises in Their Respective Intra- and Inter-subspecific Social Relations (Non-sexual) with the Other 13 Members of the Herd.

Contacts with:	P†	A	L	S	Total	Contacts	P	A	L	S	Total
♂RT vicina ♂♂	36^{2}	55^{3}	11	50^{3}	152	♂R= vicina ♂♂	28^{2}	47^{3}	11	47^{3}	133
(vic.) " ♀♀	32^{2}	26^{2}	—	—	58	(vic.) " ♀♀	28^{2}	40^{3}	—	11	79
Non " ♂♂	52^{4}	13	14	—	79	Non " ♂♂	36^{3}	25^{2}	—	—	61
" " ♀♀	11	15	11	—	37	" " ♀♀	—	—	—	—	—
Totals	131	109	36	50	326^{22}	Totals	92	117	11	58	273^{20}
♂RO vicina ♂♂	14	54^{3}	—	47^{3}	115	♂RX vicina ♂♂	22^{1}	48^{3}	—	44^{3}	114
(vic.) " ♀♀	11	11	—	15	37	(vic.) " ♀♀	19	24^{2}	—	27^{2}	70
Non " ♂♂	13	—	—	12	25	Non " ♂♂	—	—	11	—	11
" " ♀♀	14	11	—	—	25	" " ♀♀	—	—	—	—	—
Totals	52	76	—	74	202^{14}	Totals	41	72	11	71	195^{13}
♂BT vicina ♂♂	26^{2}	12	25^{2}	—	63	♂BO vicina ♂♂	41^{3}	26^{2}	—	12	79
(van.) " ♀♀	14	11	—	—	25	(van.) " ♀♀	29^{2}	—	—	13	42
van. ♀ YT	11	11	—	—	22	van. ♀ YT	—	13	—	—	13
van. ♂ BO	15	14	12	15	56	van. ♂ BT	15	14	12	15	56
YO, RH, BX	—	—	—	—	—	YO, RH, BX	—	13	—	—	13
♀ YD	—	—	—	—	—	♀ YD	11	14	—	—	25
Totals	66	48	37	15	166^{13}	Totals	96	80	12	40	228^{17}
♀RD vic na ♂♂	33^{2}	47^{4}	—	31^{2}	111	♀Y= vicina ♂♂	43^{3}	41^{3}	—	22^{2}	106
(vic) " ♀♀	—	—	—	—	—	(vic.) " ♀♀	—	—	—	—	—
Non " ♂♂	14	20^{1}	—	13	47	Non " ♂♂	43^{3}	11	—	—	54
" " —	—	13	—	—	13	" " —	12	11	—	—	23
Totals	47	80	—	44	171^{12}	Totals	98	63	—	22	183^{14}

* Number of social units indicated by superscript numerals.

† The four rest patterns are indicated thus: P = evening rest period; A = morning rest period; L = Lettuce-eating period; S = Sunning period.

pertinent to the present paper. The remaining six tortoises will be referred to indirectly, insofar as their actions relate to the eight large animals.

The males of the subspecies *vicina* differed markedly from the females of this subspecies. The intra-subspecific social contacts of the four males totalled 32 social units, averaging 16 contacts each. Each male averaged eight social units. The females, however, established no social units between themselves.

Sixteen social units (averaging 15.2 contacts each) were recorded between males and females of this subspecies, with an average of 2.6 social units per tortoise. Eleven social units were recorded between *vicina* and *vandenburghi* males. These units averaged 12.9 contacts each and two social units were the average per tortoise.

Three social units (average 11.3 contacts) were established between *vicina* males and the three small males, YO, RH and BX. Five social units (average 12.5 contacts) were noted between *vicina* males and female YD.

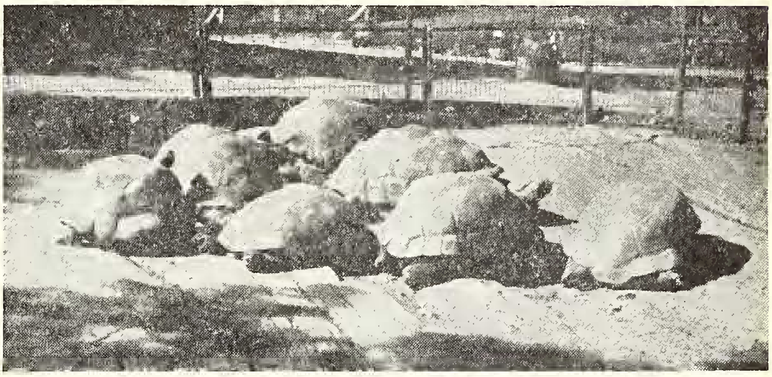
The social contacts between *vicina* females and non-*vicina* males totalled 10 social units (average 13.9 contacts). The social units between *vicina* females and non-*vicina* females totalled four (average 12.2 contacts).

It is interesting to note that the social contacts recorded between *vicina* males and *vicina* males, between *vicina* females and *vicina* males, and between *vicina* males and non-*vicina* males were almost the same, being 100, 90 and 101, respectively, in the P pattern. But in the A pattern, *vicina* males established twice as many social contacts (204) with *vicina* males as with *vicina* females (101) and five times as many as with non-*vicina* males (38) or with non-*vicina* females (40). Only two social units (average 11.0) in the L pattern were established between *vicina* males and *vicina* males; none with *vicina* females, two with non-*vicina* males (average 12.5), and one (11) with non-*vicina* females. In the S pattern the *vicina* males tallied 188 contacts between themselves or 12 social units (average 15.6). This was 3.5 times as many contacts as between *vicina* males and *vicina* females. No social units were recorded between *vicina* males and non-*vicina* males or non-*vicina* females in the S pattern.

Individual differences among tortoises were especially striking. For example, R= was rarely if ever observed in the mounting posture[4] with a female nor was he ever heard to "roar." The hoarse sound best described as "roaring" always accompanies copulatory activity. RT, on the other hand, could be heard bellowing almost every day and he mounted every female in the herd repeatedly

[4] In the mounting posture, the concavity of the plastron of the male fits over the rounded posterior portion of the female's carapace.

TEXT-FIG. 3. Typical lettuce-eating (L) pattern. Reading from left to right, in front—BT, YT; behind, RD, BO, YX, YD, YO (shown turning away).



TEXT-FIG. 4. Typical mid-morning sunning (S) pattern. Reading from left to right, in front: $R^=$, YO, RD, BO; behind, RX, RT. RO.

during the summer. Despite these differences, $R^=$ tallied six social units (average 13.1) with 79 contacts with *vicina* females, while RT tallied only four social units (average 14.5) and 58 contacts. RO also exhibited considerable sexual interest in females, yet tallied only three social units (average 12.3) and 37 contacts with *vicina* females. RX, like $R^=$, displayed little sexual interest yet he is recorded with five social units (average 14.0) and 70 contacts.

RT and $R^=$ displayed almost equal companionship (the "Kumpan" of Lorenz, 1935, 1950) toward BT and BO; each established two social units with each of the latter. RT averaged 16.2, $R^=$ 12.2 contacts per unit. RO seemed to ignore BT but made two social units (average 12.0) with BO. RX ignored both except to eat lettuce (L pattern) with BT 11 times. Both RO and RX seemed oblivious of RH, BX and YO, but RT made 11 contacts each with RH and YO; $R^=$ contacted RH 12 times but failed to contact BX or YO "socially."

It is notable that the highest number of contacts per social unit among the *vicina* males was scored between themselves (16.09); the next highest with *vicina* females (13.72); followed by 12.22 with non-*vicina* males; and lastly 12.4 with non-*vicina* females, but only by RO and RT; neither RX or $R^=$ were recorded in contact with non-*vicina* females (YD or YT).

This last observation might indicate a relationship between sexual companionship and the companionship as exhibited by the P, A, L or S patterns. RT established three social units and RO two with YD, averaging 12.4 contacts each. These two males also displayed an intense sexual interest in YD. Neither male contacted YT "socially."

It is interesting that BO contacted YD 11 times in the P, and 14 in the A, pattern; BO also contacted YD sexually. BT failed to contact YD either "socially" or sexually. Both these males showed some interest in YT. BT contacted her 11 times in both P and

A patterns while BO made contact with her 13 times in the A pattern.

With the *vicina* females, BT contacted RD 14 times in the P, and YX 11 times in the A, pattern. BO made contact with RD 13 times in the S, Y= 17 times in the P, and YX 12 times in the P pattern (Tables 2 and 4).

With RH, the saddle-back tortoise, BO made contact 13 times in the A pattern. BT ignored RH and both *vandenburghi* males made only random contacts with the males BX and YO.

During the winter months, group A (comprising RT, R=, BO, RO, RX, Y=, RD and BT) is housed in the usual summer quarters, while group B (comprising YD, YT, RH, YX, BX and YO) occupies an adjoining inside corral. A number of apparently unrelated observations fit into a pattern when the separation of the two groups in winter is considered.

For example, RD and Y= contacted the four males, RT, RO, RX and R= (all of group A) a total of 217 contacts in eight social units each (average 13.5 contacts). On the other hand, YT (in group B) contacted BT and BO (both in group A) a total of only 35 times for three social units (average 11.6 contacts). Of a total of seven social units tallied for YT, only two were with individuals in group B, namely, BX (15 times) and YX (13 times).

RH made only random contacts with other members of group B, but with members of group A, RH established 78 contacts for six social units. BX, the other saddle-back, had different social inclinations. The three social units recorded for BX were all in the A pattern, and all were with individuals from group B, fifteen times each with both YT and YX and 11 with YO. This becomes more significant when it is noted (Text-figure 2) that all four of these animals were among the last to leave the barn in the morning or had to be urged to leave by the keeper.

For YD, 98 contacts were recorded for eight social units (average 12.2 contacts), of which none were with fellow members of group B. Even though this female failed to leave the barn promptly, her contacts with others of group B in the A pattern were only at random.

In general, it might be mentioned that the anticipated sociability within group B failed to materialize. The fact that the smaller specimens had been separated from the larger ones for about six months seemed rather to heighten the interest which members of each group had for the other, with the exception of male BX.

Discussion.

The migratory instinct might well have been the psychological factor around which the social pattern of the Galapagos tortoise developed. The ebb and flow of the wet and dry seasons made necessary the seasonal movements of the animals. The almost impenetrable underbrush and rocky landscape encouraged the migrants to frequent specific routes which, with the passage of the centuries, became deeply worn trails which permitted only one-way traffic.

It is assumed that, in order that the travellers might move without interruption, some form of hierarchy developed with a leader who initiated movements and set the pace along the trail, and with a numerical order of sequence imposed upon the rest of the herd, so that each member would stay in line. An analysis of the behavior of the captive herd of tortoises revealed the presence of a hierarchy, but this was not surprising since these tortoises behaved, in some respects, similar to herds of mammals or flocks of birds in which it is well known that hierarchies occur.

It has been shown that environmental factors have been highly influential in shaping particular behavioral patterns. For example, the diet of seaweed restricts the dispersal of the Galapagos Sea Iguana, *Amblyrhynchus cristatus*, to the rocky beaches where the feeding grounds are the flats between high and low tide. As a consequence the lizards swarm along the beaches, with the females and juveniles crowded behind an imaginary barrier 30 feet above high tide-mark while the big males dwell, each in his own small plot of beach, between the females and the water. Trespassing across the boundaries of these tiny territories results in fighting to reestablish territorial ownership (Schmidt, 1935).

Corn and bean seedlings and the leaves and blossoms of fruit trees attract the Mexican Iguana, *Ctenosaura pectinata*, to the vicinity of villages where it finds refuge in the loose-rock walls surrounding the gardens. Along the stone barriers the big lizards set up individual territories. The dominating male of the colony usurps the highest vantage point and the right to "patrol" the enclosing garden wall daily; at "patrol" time the other members of the colony retreat beneath the rocks, reappearing after the dominant male has passed by. At distances removed from human habitations the iguanas are usually widely scattered, with one male patrolling a territory perhaps 100 times as large as that possessed by an individual in a colony near a village (Evans, 1951).

The crowding which often occurs with the Mexican fence lizard is due to the paucity of lookout stations, hence scattered ruins are the sites for colony formation and its accompanying hierarchy (Evans, 1946). Colony formation sometimes occurs in the western fence lizard also (Fitch, 1940), although in both species individual territories occur where the competitive pressure is less.

Cagle (1944) has shown that the aquatic turtles, *Pseudemys scripta* and *Chrysemys picta*, occupy individual territories, but because good sunning logs are scarce, territorial claims are relaxed when it is time to leave the water and rest in the sunshine.

Then as many individuals as possible crowd upon such spots for relaxation.

The relative sparsity of the Anolis lizard population of Cuba enables each male to enjoy a separate territory (Evans, 1938), while in Bimini, the Anolis population is denser, making it necessary for two or more males to occupy the same tree. When this occurs, the largest male dominates the others in the tree and a simple hierarchy is established (Oliver, 1948). When such crowding occurs in a cage, a straight line hierarchy can be created involving as many as 19 males (Evans, 1936).

Summary.

Exactly how sociability (an endogenous urge on the part of one member of a herd to be with or near to another) relates to social rank in Galapagos tortoises is not clear, but the eight largest specimens (group A) in the New York Zoological Park were more sociable than the six smaller ones (group B), and if the entrance and exit order, to and from the shelter, are considered, then the former were also higher in social rank or hierarchy.

Sociability was tested in several ways. A distinction was made between random and social contacts. Group A established 67.9% more social contacts and 12.6% fewer random contacts than group B. The greatest degree of sociability was recorded among the large males of the subspecies *vicina*. These males were successively less sociable toward *vicina* females, non-*vicina* males, non-*vicina* females. The *vicina* females were surprisingly asocial toward each other but were slightly more social toward females of other subspecies. They were most sociable toward males.

When the ratio of random contacts divided by social contacts was taken for groups A and B, the figures were 1.06 for A and 4.05 for B.

The two *vicina* males that evinced the least sexual interest were most sociable toward *vicina* females and least sociable toward non-*vicina* females. In contrast, the two most active *vicina* males, sexually speaking, were least sociable toward *vicina* females and most sociable toward non-*vicina* females.

None of the social or random contacts recorded in this report were of the mounting type associated with sexual intercourse.

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